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# THE BOTANICAL GAZETTE

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## TEMPERATURE AND LIFE DURATION OF SEEDS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 226

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(WITH FIVE FIGURES)

### Introduction

In this investigation I have sought to determine the extent to which a study of the laws of the life duration of seeds at high temperatures ( $50-100^{\circ}\text{C.}$ ) will explain the process of degeneration of air-dried seeds at ordinary storage temperatures. In this connection it seemed especially desirable to determine: (a) the temperature coefficient ( $Q_{10}$ ) for the death rate or life duration of seeds; (b) to what extent the formula which LEPESCHKIN (22) applied as a time-temperature formula for the coagulation of proteins and as a life duration-temperature formula for active living plant cells can be applied as a life duration-temperature formula to dry seeds; and (c) how far the temperature coefficient ( $Q_{10}$ ) on the one hand, and the LEPESCHKIN formula on the other, when applied to actual measurements at high temperatures serve as a means of approximating the life duration of air-dried seeds at ordinary storage temperatures. With these questions in mind a number of determinations have been made on wheat of the Turkey-red variety.

### Historical

The effects of high temperatures on dry seeds early engaged the attention of investigators. In 1875 JUST (19) showed that dried seeds of *Trifolium pratense* were killed at  $120^{\circ}\text{C.}$ , and that

at lower temperatures (time of exposure not given) the speed of germination fell with heating. HÖHNEL (17) in 1877 found that most seeds with a moisture content below 3 per cent would endure a temperature of 110–125° C. for 15 minutes. In 1902 DIXON (13) summarized the earlier work on high temperatures of seeds as follows: “(a) imbibed protoplasm resists 30–40° C. more than the optimum temperature; (b) dry protoplasm resists 100° C. more than the optimum temperature of the protoplasm of imbibed seeds.” DIXON found that the time required for germination was lengthened as the temperature increased, and that each seed had a heat point at which the time of germination began to increase. In 1899 JODIN (18) found that 30–60 per cent of desiccated seeds of peas and cress may be exposed to a temperature of 98° C. without losing their ability to germinate, if first dried at 60° C. for 24 hours and then heated to 98° for 10 hours.

The cause of the loss of viability in old seeds has been a matter of considerable discussion and investigation. DUVEL (14) states that seeds retain their viability longest in conditions which permit least respiration, implying that the food materials are exhausted. ACTON (1), by a careful analysis of old and new seeds, found that there was but a slight difference in their food content. In the course of these investigations he discovered that there was considerable diastatic and proteolytic enzyme action in new seeds, while in old seeds there was none. He assumed, therefore, that the loss of viability is related to the loss of enzyme activity. The investigations of THOMPSON (31), WAUGH (32), and others furnish some evidence for this conclusion. They found that old seeds with a low percentage of germination, when soaked in enzyme solution, showed an increase in viability. BROCC-ROUSSEAU and GAIN (8, 9, 10, 11) in their earlier work found that enzymes gradually disappear with age. They tested 300 species of seeds and found no peroxidases in any of the samples secured before the eighteenth century. In the case of *Triticum* they found enzymes in samples as old as 200 years. In some cases the retention of enzymes was attributed to the hard coats of the seeds, and the loss of viability was stated to be due to some cause other than degeneration of enzymes. ASPIT and GAIN (3) found enzyme activity in seeds

long dead and in seeds killed by anesthetics. Miss WHITE (33) found no increase in the germination of seeds soaked in enzyme solutions, but rather a decrease due to an increased fungal action. She found the life duration of *Triticum* to be 17 years, with no loss of enzyme activity. According to her work the enzyme theory of the loss of viability is not tenable.

Some very significant work has been done on the time-temperature relation of coagulation of protein both in vitro and in the living cell. BUGLIA (7) found that the time required for the coagulation of blood serum varies with the temperature used. The time of coagulation was found to be a logarithmic function of the temperature. CHICK and MARTIN (12) found that the time required to precipitate egg albumen and haemoglobin from solution varies with the temperature and with the concentration of the solution. LEPESCHKIN (22) showed that the death of active plant cells by supramaximal temperatures is due to the coagulation of the cell protoplasm. He applied a logarithmic formula to express the relation of temperature to the time of coagulation of proteins in vitro as well as in the living cell. By the application of this formula to the determined time for coagulation at any two temperatures, one can calculate the time necessary for coagulation at any other temperature. On this basis LEPESCHKIN calculated the life duration of active *Tradescantia* cells at 20° C. to be 33 days, and at zero to be 3 years. He believes that the life duration of plant cells is very much longer than indicated because of a redispersal process, carried on by the active living cells, which counteracts the coagulation process.

The results of many workers in this field have been well summarized in a recent monograph by KANITZ (20), who has brought together the literature from several related subjects. He shows that in general the effect of temperature upon the rate of chemical processes is governed by the Van't Hoff law, that is, the coefficient for a rise in temperature of 10° C. ( $Q_{10}$ ) is 2 to 3. From the experimental results at any two temperatures the value of  $Q_{10}$  may be calculated from the following equation (referred to as formula 1 and formula 2):

$$Q_{10} = \left( \frac{k_2}{k_1} \right)^{\frac{10}{t_2 - t_1}} \text{ or } Q_{10} = 10^{\frac{10 (\log k_2 - \log k_1)}{t_2 - t_1}}$$

in which  $k_2$  is the rate of reaction obtained at temperature  $t_2$ , and  $k_1$  the rate of reaction obtained at temperature  $t_1$ .

Many processes in living organisms show a temperature coefficient approximately that of the Van't Hoff law within certain temperature limits. Some of these show high values of  $Q_{10}$  at lower or at critical temperatures. High values of  $Q_{10}$  are found also for life duration and for coagulation or denaturing of proteins.

KANITZ (20) brings out more clearly the relation of temperature to the rate of life processes by recalculating  $Q_{10}$  at the various temperature intervals instead of giving only the average coefficient for the whole temperature range. In this way it is found that in many cases  $Q_{10}$  is not a constant at all intervals of temperature, but shows decreasing values with rise of temperature.

### Method

In order to obtain constant temperatures for heating the seeds, a thermostat was devised as shown in fig. 1. It consisted of an external water bath heated by an electric stove. In this bath was placed a similar vessel of smaller dimensions which was closed at the top and connected with a water-cooled reflux condenser. Methyl or ethyl alcohol or mixtures of methyl or ethyl alcohol with water was used for temperatures 64–99° C. The temperature during the time of an experiment showed a fluctuation of less than  $\pm 0.1$  C. For lower temperatures, where the time was much prolonged, the usual water-jacketed incubator was used. This was well wrapped with heavy woolen blankets. The temperature of the incubator was regulated by the automatic electric apparatus devised by LAND (21). It gave a very equable temperature, showing a straight line on the drum of an ordinary recording thermometer.

The seeds were heated in the thermostat by inserting securely corked test tubes, each containing 100 selected seeds, through perforations in the top of the inner vessel. These test tubes were suspended by threads passed through the perforations, and the threads were then secured by corks which closed the openings.

Many of these tubes were inserted at the same time and removed in duplicate at successive intervals. Seeds were heated in the

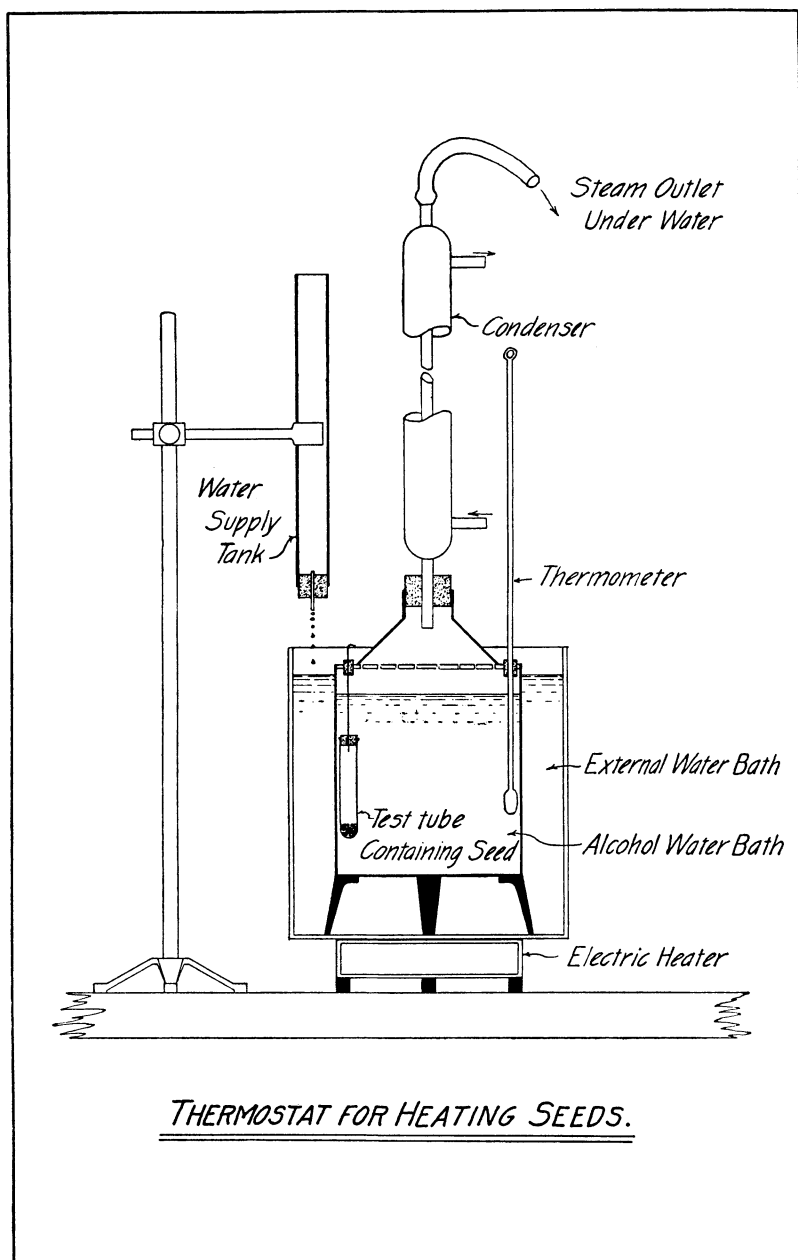


FIG. 1

incubator in a similar manner by inserting the tubes through perforations in the top. This avoided the main source of temperature fluctuation in the incubator, opening the door.

After the seeds were heated they were sterilized by washing for 2 or 3 minutes in a  $n/50$  solution of silver nitrate. While in this solution the seeds were stirred thoroughly in order to free them of all air bubbles. Then they were washed thoroughly in sterile distilled water to remove the excess of silver nitrate which would injure the seedlings when germinated. SCHROEDER (28, 29) has shown that the seed coat of wheat is only slightly permeable to silver nitrate, and many parallel tests with treated and untreated seeds confirmed his conclusions. The importance of sterilizing the seeds is realized when we consider that in some cases the germination was delayed as much as 20 days. Miss MÜLLER (25), in her work on germination of heated seeds, found that after 10 days seeds were either germinated or destroyed by mold. By sterilizing the seeds and the germinating dishes and using some care in planting, cultures were kept practically free from fungal growth for several weeks.

After sterilizing and washing, the seeds were germinated in large Petri dishes containing a layer of moist cotton covered with a layer of filter paper. The dishes were sterilized at  $140^{\circ}\text{C.}$ , and considerable care was used in planting the seeds to maintain sterile conditions. The dishes were kept in laboratory light and temperature, and their daily progress in germination was noted.

The moisture content of the seeds was tested from time to time, and only very slight variations occurred in any one of the 3 moisture content experiments. The DUVEL (15) method was used parallel with the ordinary oven drying method and the two gave concordant results. Since the DUVEL method requires less than an hour to make a test, it was possible to check the moisture content before filling the tubes for each trial.

### Results

The effects of heating seeds is well shown in table I, which is a daily record of the germination of a time series heated at  $87^{\circ}.5\text{ C.}$  Seeds were considered normally germinated when both root and

stem had broken through the seed coat. When only the root or the shoot appeared, the seeds were considered partially germinated. Partial germination is represented in this table by the figures in small type. The delay in time of germination as the time of exposure increased is strikingly shown here. The controls usually

TABLE I

<i>Record Sheet No. 21</i> <i>Temp: 87.5°C. Moisture: 12%</i>										<i>Turkish Red Wheat</i> <i>April 10, 1914.</i>									
<i>Time</i> <i>Days</i>	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
<i>Control</i>	0	2	2	4	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0
	92	92	92	93	95	95	98	98	98	98	98	98	98	98	98	98	98	98	98
<i>7 Min.</i>			0	15	12	7	8	7	8	7	5	3	3	4	4	4	3	2	
			2	5	27	41	49	55	61	64	67	70	72	72	72	72	73	74	
<i>8 Min.</i>					4	8	8	7	8	7	5	3	1	5	1	1	1	0	
					5	10	25	30	35	41	47	52	54	54	58	59	59	60	
<i>9 Min.</i>						2	4	4	5	4	5	4	5	2	3	6	5	4	
						2	4	8	10	11	18	25	28	32	34	35	37	38	
<i>10 Min.</i>		<i>Per Cent Partially Germinated</i>									1	3	4	6	4	3	4	5	
		<i>Per Cent Germinated</i>									0	0	0	0	4	5	9	11	11
<i>11 Min.</i>												1	1	0	0	1	2	1	
												1	1	2	4	4	4	5	
<i>12 Min.</i>													2	2	2	2	2	2	
													0	0	0	2	2	2	
<i>13 Min.</i>																			
																0	0	0	

germinate in about 2 days, while some of the treated seeds were delayed for 18–20 days. The relation between time of heating and the percentage of germination is shown in the table. There is a gradual decrease in the percentage of germination with increased time of heating. After the delayed seeds germinate their growth is much slower than that of unheated seeds. It should be noted that the effects here of heating are similar to those produced by the aging of seeds stored at room temperature. This indicates



that there may be a similar change in the two cases. The change occurs rapidly at the high temperature, but slowly at the low temperature.

Some investigators have used the time required to kill all seeds as the end point. In this work we have selected the time required to kill 75 per cent of the seeds as the end point. This is more desirable because there seems to be considerable discrepancy in the resistance of a few stronger seeds. This end point for 12 per cent moisture and various temperatures was obtained as shown in table II. While there are some irregularities, there is a definite relation between temperature and time of exposure necessary for killing 75 per cent of the seeds.

The time-temperature formula suggested by LEPESCHKIN (22) has been used here to calculate the life duration of the seeds. By determining the time required to kill seeds at any two definite temperatures, the time for killing seeds at any other temperature can be calculated. The formula (referred to as formula 3) is:

$$T = a - b \log Z$$

in which  $T$  is the temperature in degrees Centigrade,  $Z$  is the time in minutes, and  $a$  and  $b$  are constants. If the loss of viability of seeds during storage is a matter of coagulation of cell proteins of the embryo, this time-temperature formula for the coagulation of proteins should be applicable as a temperature-life duration formula for seeds. In experiment the life duration determined must be at relatively high temperatures, ranging from 50 to 100° C. for air-dried seeds.

In formula 3 constants  $a$  and  $b$  may be calculated by substituting the time and temperature of any two trials and solving for  $a$  and  $b$  in the two equations. This is the method of calculation used by LEPESCHKIN (22). In order to weigh all determinations equally, the constants in this paper are calculated by the method of least squares. The values of the constants and the life duration found in each experiment were substituted in the equation and the theoretical temperatures were calculated. The values are shown in table II. A comparison of these found and calculated temperatures shows that a comparatively close agreement exists. The discrepancies are within the limits of experimental error.

Fig. 2 is a time-temperature curve representing the experimental data shown in table II for wheat with 12 per cent

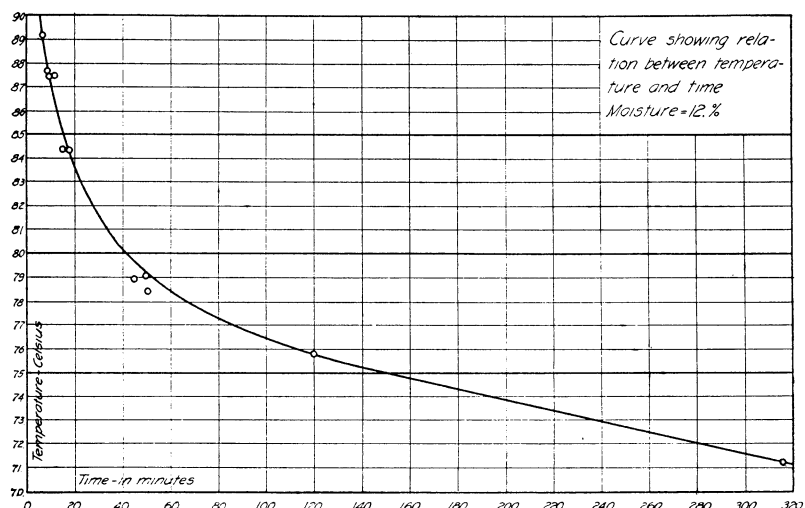


FIG. 2

TABLE II

Germination record of Turkey-red wheat 12 per cent moisture; theoretical temperature calculated by the formula  $T = a - b \log Z$ ;  $T$  is temperature (Centigrade);  $Z$  is time in minutes;  $a$  and  $b$  are constants;  $a = 96.87$ ;  $b = 10.4$ ; value of  $Q_{10}$  as calculated by method of least squares = 10.14.

Time in minutes	Calculated temperature	Experimental temperature	$Q_{10}$
7.....	88.1° C.	89.2° C.	6.09 (10.3)
8.....	87.5	87.7	
9.....	87.0	87.5	
10.....	86.5	87.5	
15.....	84.6	84.4	
18.....	83.7	84.4	12.94 (7.6)
45.....	79.7	78.9	
50.....	79.2	79.1	
50.....	79.2	78.5	
120.....	75.2	75.8	
315.....	70.9	71.3	

Predicted life duration: 50° C., about 22.3 days; 25° C., about 15.5 years; 20° C., about 46.9 years; 0° C., about 393 years.

moisture. The ordinates represent degrees Centigrade and the abscissae minutes of time. Except for the irregularities which

occur at 78 and 79°, there appears a marked agreement in the data and the points representing the experimental data approximate a smooth curve. Table II shows the value of  $Q_{10}$  for experimental temperatures as calculated by formula 2. In tables II-IV partial germination is represented by the figures in parentheses.

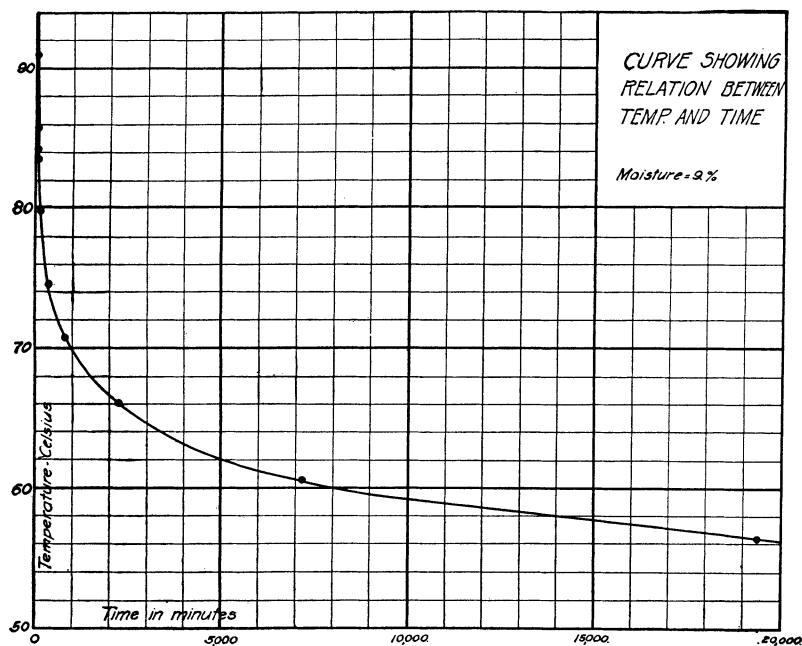


FIG. 3

Table III shows the found and calculated data for wheat with 9 per cent moisture. The calculated temperatures were obtained by the same method as those in table II, and here as before there is a close agreement between the theoretical and observed values. In fig. 3 the experimental data of table III are also expressed in a time-temperature curve. Practically all of the points representing the experimental data fall on a smooth curve. Table III shows the value of  $Q_{10}$  for experimental temperatures as calculated by formula 2.

Table IV shows a limited number of data for wheat with 17.5 per cent moisture. As would be expected, the time required to

TABLE III

Germination record of Turkey-red wheat 9 per cent moisture; theoretical temperature calculated by formula  $T=a-b \log Z$ ;  $T$  is temperature (Centigrade);  $Z$  is time in minutes;  $a$  and  $b$  are constants;  $a=100.8$ ;  $b=10.4$ ; value of  $Q_{10}$  as calculated by method of least squares=9.23.

Time in minutes	Calculated temperature	Experimental temperature	$Q_{10}$
8.....	91.4° C.	90.8° C.	13.49 (11.0)
27.....	85.9	85.7	
45.....	83.6	84.2	
63.....	82.1	83.5	
140.....	78.5	79.8	7.03 (9.0)
435.....	73.4	74.4	
810.....	70.5	70.8	8.51 (10.2)
2340(1.6 days).....	65.7	66.0	
7200(5.0 days).....	60.6	60.6	
19440(13.5 days).....	56.2	56.3	

Predicted life duration: 50° C., about 53.4 days; 25° C., about 37.3 years; 20° C., about 111.2 years; 0° C., about 938.5 years.

kill such seeds at the temperatures used in the former experiments is exceedingly short. The error due to the time required for the

TABLE IV

Germination record of Turkey-red wheat 17.5 per cent moisture; theoretical temperature calculated by formula  $T=a-b \log Z$ ;  $T$  is temperature (Centigrade);  $Z$  is time in minutes;  $a$  and  $b$  are constants;  $a=81.73$ ;  $b=8.04$ ; value of  $Q_{10}$  as calculated by method of least squares for last 4 temperatures=16.45.

Time in minutes	Calculated temperature	Experimental temperature	$Q_{10}$
3.0.....	77.9° C.	87.1° C.	2.22 (7.6)
3.75.....	77.1	83.6	
4.0.....	76.9	83.1	
5.5.....	75.8	79.5	
8.0.....	74.5	74.7	4.90 (9.0)
23.0.....	70.8	70.5	
140.0.....	64.5	64.4	19.71 (9.9)
440.0.....	60.5	60.6	

Predicted life duration: 50° C., about 6.1 days; 25° C., about 21.6 years; 20° C., about 64.4 years; 0° C., about 2800 years.

seeds to attain the temperature of the bath is therefore very apparent here. The data of this table are expressed also as a time-

temperature curve in fig. 4. Here again there is close agreement between the found and the calculated values. Table IV shows the value of  $Q_{10}$  for experimental temperatures as calculated by formula 2.

In fig. 5 the temperature is plotted against the logarithm of the time for wheat with 9, 12, and 17.5 per cent moisture. Since one of the constants is found to have a common value in the 9' and 12

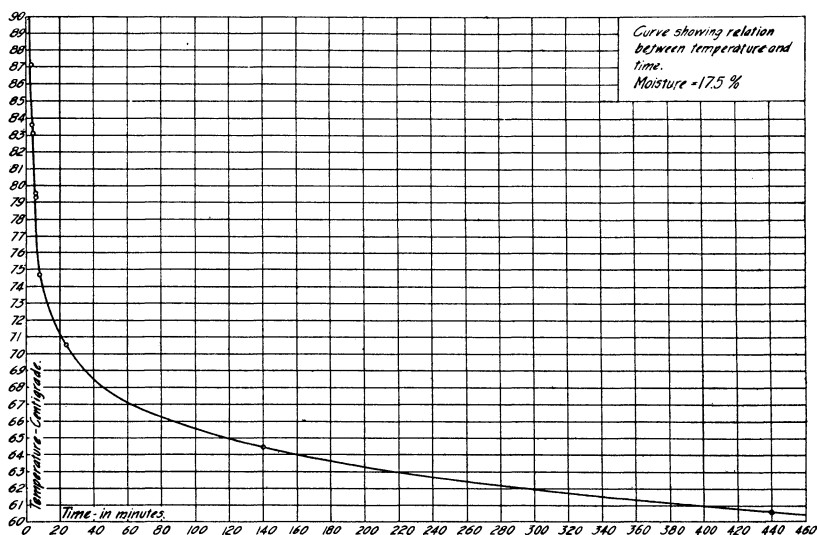


FIG. 4

per cent moisture curves, they are parallel. Since they were obtained under identical conditions, one may surmise that the curves in which temperatures in degrees Centigrade are plotted against time in minutes are parallel. Sufficient data are not available with the 17.5 per cent moisture content at experimentally reliable time intervals to justify a conclusive generalization. The curve for the 17.5 per cent moisture content deviates upward from a straight line in the lower time range. This is due to the fact that a considerable part of the short period of exposure was consumed in heating the seed up to the temperature of the bath.

## TEMPERATURE COEFFICIENT

The temperature coefficient ( $Q_{10}$ ) of the life duration of wheat was found to vary with the moisture content. The average value for 9 per cent moisture, calculated by the method of least squares, is 9.23; for 12 per cent moisture, 10.14; and for 17.5 per cent moisture, 9.83. GOODSPEED (16), working with barley grains, found a coefficient varying from 10 to 16 as calculated by KANITZ (20). The result obtained by GOODSPEED is marred by the lack

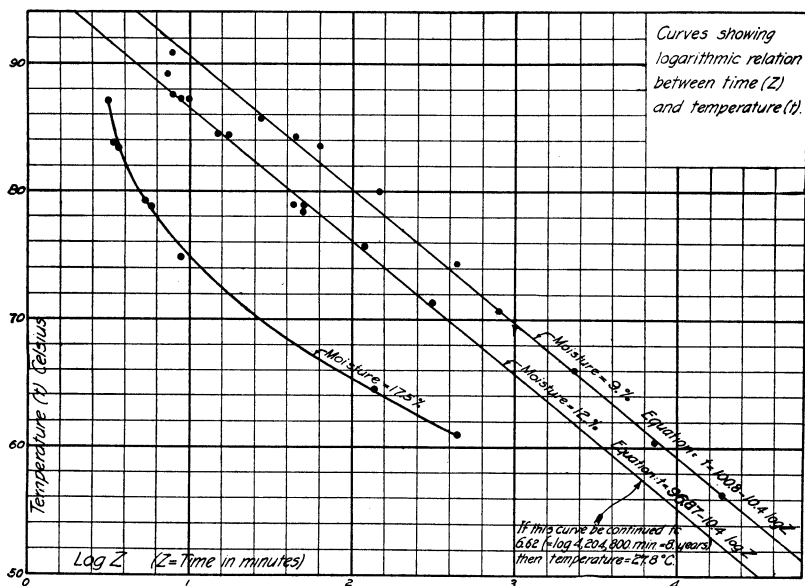


FIG. 5

of determination and control of the moisture content. Since the seeds were soaked for only one hour previous to heating, they had not absorbed the maximum amount of water. Such seeds, when heated in water at various temperatures for various periods of time, show considerable difference in their water content. I find by calculation, according to formula 2, that LEPESCHKIN'S data on *Tradescantia discolor* give a value of about 5.0 for  $Q_{10}$ , and on *Beta vulgaris* from 2.5 to 10.4. AYRES (4), in a recent investigation on one of the red algae (*Ceramium tenuissimum*), found an

average coefficient of 1.47 per degree Centigrade. I have calculated his data according to formula 2 and find the value of  $Q_{10}$  to vary from 5 to 88. There is a definite break in his data which prevents them from falling on a smooth curve. This is probably due to some uncontrolled factor in experimentation. I find that the data in other articles cited here, both on life duration and coagulation of proteins, give smooth curves.

The  $Q_{10}$  coefficient for life duration of animals, so far as worked, is very much larger than for plants. LOEB (23) found a  $Q_{10}$  value varying from 240 to 1450 for fertilized sea urchin eggs, while for unfertilized eggs he found a value of 600. MOORE (24) found a  $Q_{10}$  value varying from 485 to 3900 for the stems of *Tubularia crocea*.

The  $Q_{10}$  value for the coagulation of proteins shows a wide variation for the various proteins or different conditions of the same protein as calculated by KANITZ (20). CHICK and MARTIN (12) found a value of 14 for haemoglobin and 635 for egg albumen. I have calculated the value of  $Q_{10}$  for BUGLIA'S (7) data and find it to be about 15 for blood serum, 760 for fresh muscle, 45 for neutral albumen, and 240 for neutral concentrated albumen.

The low  $Q_{10}$  coefficients found for plants mean that they can endure various supramaximal temperatures for relatively long periods as compared with animals with the larger  $Q_{10}$  coefficients. This may be of great importance to plants, since in many habitats they are unable to avoid intense radiant energy. The radiant energy is largely absorbed and the plants attain temperatures as much as 28° C. above the air temperatures, and certainly several degrees above the maximal for growth (2, 6, 26, 30). In general the animal is able to avoid such superheating through locomotion. As bearing on this point many more determinations are needed both on animals and on plants of a variety of habits and habitats.

The difference between the temperature coefficients for plants and animals shows itself in an experimental way. There is the possibility of employing a much greater range of temperature in plant material. In the investigations on animals previously cited the range used is about 10° C., while in investigations on plants the range is 20° C. or more. In plants a much greater range

would be possible were it not for the fact that the small coefficients give life durations too long for convenience in experimentation at temperatures not considerably above the maximum.

The difference between plants and animals in the size of the coefficients manifests itself in another way. In the investigations with animals the temperatures used are largely below  $45^{\circ}\text{C.}$ , while with plants it is not uncommon to use temperatures above  $70^{\circ}\text{C.}$  and obtain an easily measurable life duration. The maximum temperature usable is determined also in part by other factors, such as percentage of water present and the general attunement of the particular plant to the temperature. The lower the percentage of water in the seed, the higher the temperature that can be used with it. It is probable also, that in forms like *Ulothrix* and *Hydrurus*, having maxima below  $24^{\circ}\text{C.}$  (27), the possible experimental temperatures would not run so high.

### Discussion

The rather close agreement between calculated and found values indicates that the time-temperature formula for the coagulation of protein can be applied as a temperature-life duration formula for seeds, at least under the conditions of these experiments. It is probable that the accumulation of more data will make it possible to find some other equation which expresses more adequately the relationship between the variables involved. In the experiments on wheat of 9 and 12 per cent moisture the average deviation of the observed from the calculated temperatures is less than 1 per cent. The corresponding average deviation for the 17.5 per cent moisture content is about 8 per cent. The unexpectedly large error with the 17.5 per cent moisture content is due to the previously noted fact that a considerable part of the time of exposure is consumed in heating the seeds up to the temperature of the bath. The uniformly increasing deviation of the observed temperatures with short periods of time shows that greater accuracy is possible with long time exposures.

While in many reactions there is a consistent decrease in the value of the coefficient  $Q_{10}$  as the temperature increases, we do not find such a trend here. Compared with animal tissue, the value of



the coefficient is small and compares in magnitude with the value found by other workers on plant tissue. The range in the value of the coefficients is small, as indicated by the fact that the data fall on comparatively smooth curves. The coefficient  $Q_{10}$  as calculated from the data (for 12 per cent moisture) in table II by the method of least squares is 10.14. When the temperature and time-differences in formula 2 are so small that they are comparable with the errors of observation, then the numerical evaluation of  $Q_{10}$  becomes highly inaccurate. But when the time and temperature differences are large enough to render ineffective the errors of observation, then the calculated coefficient  $Q_{10}$  is comparable with the value obtained by the method of least squares.

The coefficient  $Q_{10}$  for 9 per cent moisture content was found to be 9.23 as calculated by the method of least squares from the data in table III. Similarly, the coefficient for 17.5 per cent moisture content was found to be 16.45 when calculated by the same method, using the 4 highest time observations in table IV. The 4 lowest time observations were ignored on account of the inaccuracy introduced by the time required for the seeds to attain the temperature of the bath, as previously explained.

A number of longevities have been calculated by formula 3 for the low temperatures at different moisture contents. With the relatively short range of temperatures used in these experiments, considerable error may appear in predicted longevities, especially at low temperatures. When such calculated longevities are compared with observed values, they are found usually to be considerably too large, indicating that other processes may also be effective in causing loss of viability. Since hard-coated seeds have long vitality records, it seems quite possible that this is related to the absence of oxygen and low water content.

Much more work is needed to determine how nearly one can thus approximate longevities from measurements made at high temperatures. Determinations should be made on the life duration of seeds with low moisture content. Also similar determinations should be made for a long-lived seed, such as sweet clover, for which we have reliable records of longevity, as well as short-lived

seeds, such as *Drosera*, willow, and poplar. A series of determinations should also be made on seeds at constant temperature with variations in moisture content to ascertain the relations existing between moisture content and life duration.

The data show that the LEPESCHKIN formula applies as a temperature-life duration formula for seeds at the temperatures used in these experiments, but there are several considerations that may limit its application at lower temperatures, including ordinary storage temperatures. (1) Increase of acidity of seeds will hasten the coagulation of the cell proteins; such a change is known to occur in the seeds of certain Rosaceae (15a), at least if stored in the imbibed condition. (2) LEPESCHKIN (22) found that in active plant cells a redispersal of cell proteins is going on coincidentally with coagulation. As a consequence, at high temperatures where the coagulation was rapid, the found and calculated life durations agree closely; while at lower temperatures, where redispersal is prominent, the calculated life durations are much shorter than the found values. In seeds the calculated values are usually much greater than records of longevity at room temperatures. This indicates that the redispersal process is not going on in relatively dry seeds, or, if it is, it is more than counteracted by some other process. (3) A slight error in the value of the constant  $b$  in formula 3 will give a relatively large absolute error for a life duration at low temperatures such as  $0^{\circ}$  C. At higher temperatures the absolute error becomes less. (4) The lower the water content of seeds, the more heating they withstand and the greater the longevity at moderate and lower temperatures. This law has its limits, for excessive drying is itself injurious. In seeds that will endure desiccation, injury sets in with a reduction of the water content considerably below 2 per cent, while in forms like *Drosera* it appears before air-dry condition is reached. The formula, of course, is limited to degrees of desiccation less marked than those producing injury. (5) It is possible that slow oxidation may limit the longevity of seeds. If this be true, hard seeds with their coats impervious to gases along with their constant low percentage of water are in an especially favorable condition for the

marked longevity which they show. Wheat seeds stored in absence of oxygen might give longevitys more comparable with calculated values.

### Summary

1. The life durations of wheat with 9 per cent moisture at the various temperatures are:

Life durations in minutes.....	8	27	45	63	140	435	810	2340	7200	19440
Temperatures in degrees Centigrade...	90.8	85.7	84.2	83.5	79.8	74.4	70.8	66.0	60.6	56.3

2. The life durations for 12 per cent moisture are:

Life durations in minutes. . .	7	8	9	10	15	18	45	50	50	120	315
Temperatures in degrees Centigrade.....	92.2	87.7	87.5	87.5	84.4	84.4	78.9	79.1	78.5	75.8	71.3

3. The life durations for 17.5 per cent moisture are:

Life durations in minutes.....	3.0	3.75	4.0	5.5	8.0	23.0	140.0	440.0
Temperatures in degrees Centigrade	87.1	83.6	83.1	79.5	74.7	70.5	64.4	60.6

4. The application of the LEPESCHKIN formula at high temperatures as checked by actual measurements gives an average error of 0.6 per cent for 9 per cent of moisture; 0.8 per cent for 12 per cent of moisture; and 8.25 per cent for 17.5 per cent of moisture.

5. The data available for testing the application of the formula at storage temperatures are exceedingly limited. WHITE found that 25 per cent of wheat would grow after being stored for 8.5 years. Assuming that they were exposed to an average temperature of 20° C. and had an average moisture content of 12 per cent according to formula 3, applied to the experimental data of this paper, they should have a life duration of 15.5 years. However, since the variations and averages of temperature and moisture, together with other conditions, are not known, we are not justified in pushing comparisons too far.

6. No definite trend appears in the value of the coefficient  $Q_{10}$  and its range is confined to rather narrow limits. For wheat with 9 per cent moisture the range varies from 5.6 to 16.9 with an average of 9.23; for 12 per cent moisture the range varies from 4.8 to 12.6 with an average of 10.14; while for 17.5 per cent the range varies from 2 to 20 with an average of about 10 for the whole scope of the experiment.

7. Since the range of temperature used in these experiments is comparatively short, we are not justified in placing too much emphasis on predicted longevities at low temperatures. Such longevities as have been calculated by formula 3 are large when compared with observed longevities by WHITE and others.

8. This work shows possibilities of throwing some light on the nature of the processes of the loss of viability in seeds in storage conditions. It also makes possible a quantitative statement of the significance of various storage conditions, especially moisture content and temperature, upon the longevity of seeds.

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